REPRODUCTIVE BIOLOGY OF SHRUBSTEPPE PASSERINE BIRDS: GEOGRAPHICAL AND TEMPORAL VARIATION IN CLUTCH SIZE, BROOD SIZE, AND FLEDGING SUCCESS[1]

JOHN T. ROTENBERRY

Department of Biological Sciences, Bowling Green State University, Bowling Green, OH 43403

JOHN A. WIENS

Department of Biology and Natural Resource Ecology Laboratory,
Colorado State University, Fort Collins, CO 80523

Abstract. We investigated geographical and temporal variation in clutch size, brood size, and fledging success in three common passerine species in shrubsteppe habitats of the northern Great Basin of western North America. Over a 2-year period we surveyed three vegetationally similar sites spanning a latitudinal gradient of 650 km (the geographical component), one of which we sampled for five consecutive years (the temporal component).

Clutch sizes of Sage (*Amphispiza belli*) and Brewer's (*Spizella breweri*) sparrows did not differ significantly among sites, but brood sizes and (for Brewer's Sparrow) fledging success did. These geographical differences were associated with site-specific variation in nest-predation rates and were attributed to differences in the abundances of snakes. Nests at a site in central Oregon that lacked snakes suffered virtually no predation during the 2-year geographical sampling, whereas nests in southeastern Washington and northern Nevada suffered significantly higher rates (40% and 93%, respectively).

During the 5-year temporal sampling at the central Oregon site, all measured reproductive parameters of Sage and Brewer's sparrows and clutch size in Sage Thrashers (*Oreoscoptes montanus*) varied significantly. Although the region experienced extremes of precipitation during this period, in Sage Sparrows only brood size was significantly correlated with rainfall during the previous winter. The principal source of variation in Sage Sparrow final reproductive success was predation, which peaked during an outbreak of Townsend's ground squirrels (*Spermophilus townsendi*) in 1979. This ground squirrel irruption appeared to be triggered by a pattern of a drought year followed by two relatively wet years, beginning in winter 1976–1977. Although Brewer's Sparrows also experienced considerable predation pressure in 1979, clutch size, brood size, and fledging success were significantly correlated with winter precipitation. No component of Sage Thrasher reproduction was associated with climatic variation.

The relationship between avian reproductive success and precipitation in arid regions is more complex than the traditional view of desert birds responding directly to increased primary and secondary productivity; such relationships are indirectly influenced by the effects of rainfall on predator populations, and are further complicated by time lags (up to 2 years) in predator response.

Key words: *Reproductive biology; Brewer's Sparrow; Great Basin; indirect effects; nest predation; Sage Sparrow; Sage Thrasher; shrubsteppe; Townsend's ground squirrel.*

INTRODUCTION

Knowledge of reproductive parameters such as clutch size or nesting success is important in un-

derstanding features of the ecology and evolution of birds. Variation in clutch size can influence the dynamics of population numbers, and interindividual differences in reproductive success may provide the raw material for evolutionary change. It is equally evident that, at least for
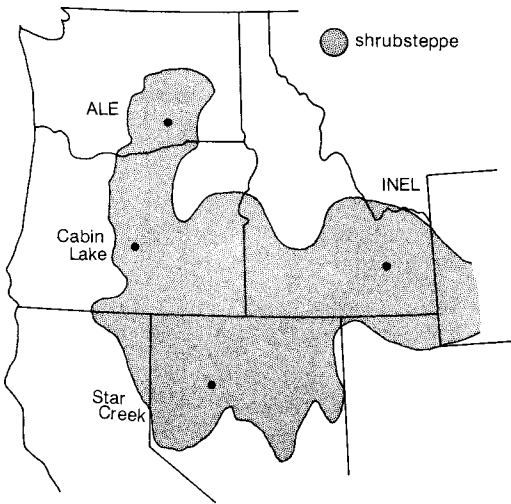
FIGURE 1.   General extent of sagebrush-dominated shrubsteppe habitat in northwestern United States and locations of study sites.

some species, these parameters vary through space and time (Ricklefs 1969). Latitudinal gradients in clutch size, for example, are a well-documented feature of many species (Wagner 1957, Klomp 1970, Murphy 1978), and "good" and "bad" years of nesting success have been detected in many studies (e.g., Lack 1943, Verner 1965, Nolan 1978, Petrinovich and Patterson 1983, Blancher and Robertson 1985).

In this paper we consider variation in spatial and temporal components of reproductive biology of three species of passerines that are found throughout shrubsteppe habitat in the northern Great Basin of North America. These species are characteristic of the avifauna of sagebrush (Artemisia)-dominated ecosystems (Braun et al. 1976, Rotenberry and Wiens 1978, Wiens and Rotenberry 1981, Ryser 1985). Shrubsteppe vegetation covers roughly 45 million hectares in western North America, and often occurs in vast, relatively unbroken tracts (West 1983). Annual precipitation in this arid region is erratic and highly unpredictable (Wiens 1974), increasing the likelihood that abiotic factors that may indirectly influence reproductive success (e.g., the direct effects of precipitation on primary and secondary production) will vary over biologically significant ranges.

We have three specific objectives: (1) to describe the geographical and temporal variation present in three discrete, meristic reproductive

attributes of the species: clutch size (the number of eggs laid), brood size (the number of chicks hatched), and "fledge" size (the number of chicks fledged); (2) to identify processes that may be responsible for producing any variation observed; and (3) to discuss briefly the implications of this variation and its causal processes for the ecology of these species.

METHODS

SPECIES AND STUDY SITES

We conducted our investigations in the cold, semi-arid shrubsteppe, which occupies a considerable portion of the northwestern United States (Fig. 1). Big sagebrush (Artemisia tridentata) is the dominant shrub of this habitat type, with rabbitbrush (Chrysothamnus spp.), antelope bitterbrush (Purshia tridentata), and saltbush (Atriplex spp.) occurring in lesser amounts. Principal grasses include representatives of the genera Agropyron, Festuca, Sitanon, and Bromus (Daubenmire 1970, Franklin and Dyrness 1973).

The most abundant breeding bird species throughout much of this area is the Brewer's Sparrow (Spizella breweri), a small (10 g) emberizid finch. Where Brewer's Sparrows are present, their densities usually range between 150–300 individuals/km^2, but may occasionally exceed 500 (Wiens and Rotenberry 1981). Although often abundant in shrubsteppe, the species is not confined to it and may be found breeding in other habitats as well (e.g., balsam-willow; Paine 1968).

Much more restricted in its vegetational associations is the Sage Sparrow (Amphispiza belli), which in the northern Great Basin is usually found breeding only in sagebrush habitat (Miller 1968). An emberizid about twice the size of Brewer's Sparrow, Sage Sparrows usually achieve densities second only to Brewer's Sparrows, ranging from 50–200 individuals/km^2 (Wiens and Rotenberry 1981, Wiens et al. 1987). Where Brewer's Sparrows are absent, Sage Sparrows are the numerically dominant species in the bird community.

Like Sage Sparrows, Sage Thrashers (Oreoscoptes montanus: Mimidae) in this region are restricted to sagebrush habitat during the breeding season (a "sagebrush obligate" according to Bent [1948]), where their densities rarely exceed 30 individuals/km^2 (Wiens and Rotenberry 1981). Unlike Sage Sparrows, however, Sage

TABLE 1.   Abiotic and biotic features and site-visitation dates of the three areas considered in this study. Plot 1 at a site is in sagebrush-dominated vegetation; plot 2 is in a second habitat type characteristic of the surrounding region (which differed among sites). Data from Wiens et al. (1987) and unpublished observations.

	ALE		Cabin Lake		Star Creek	
Elevation (m)	450		1,360		1,450	
Latitude (°N)	46°25'		43°30'		40°40'	
July temperature (mean °C)[a]	24.8		15.9		23.7	
Mean precipitation (cm):						
Annual	16.5		26.6		16.7	
Bioyear[b]	11.7		18.8		11.4	
Plot	1	2	1	2	1	2
Vegetation coverage (%):						
Grass	62	69	24	26	39	8
Sagebrush	17	8	19	18	23	2
Other shrubs	0	0	13	5	2	31
Species densities (individuals/km²):						
Sage Sparrow	207	121	69	62	78	22
Brewer's Sparrow	0	0	177	162	14	132
Sage Thrasher	0	0	37	29	0	19
Site visitation dates:						
1976	4/11–5/4, 5/27–6/21		5/12–5/19, 6/29–7/20		4/30–5/8, 6/13–6/27	
1977	4/15–4/27		6/6–7/10		5/24–6/6	
1978			6/6–7/12			
1979			5/30–7/19			
1980			5/31–7/15			

[a] Weather station locations: ALE = Arid Lane Ecology Reserve, Washington; Cabin Lake = Fremont, Oregon; Star Creek = Imlay, Nevada.
[b] October–April.

Thrashers are not confined to the Great Basin and may be found breeding in high densities in sagebrush as far east as central Montana (Feist 1968). Adults weigh approximately 45 g.

These three species share several attributes of their reproductive biology. All are summer residents at our study sites (Fig. 1), arriving to breed in early spring (exact times depend upon latitude and elevation), and have departed for the winter usually by mid- to late September. Individuals of each species construct nests either in or under shrubs (primarily *A. tridentata* at our sites), and show a preference for taller and/or denser plants (Rich 1978, 1980; Petersen and Best 1985a, 1985b). Adults are primarily insectivorous during the breeding season (Wiens and Rotenberry 1979, Rotenberry 1980), and nestlings of all three species are fed arthropods almost exclusively (Petersen and Best 1986; Rotenberry and Wiens, unpubl.).

To estimate the geographical component of variation in reproductive parameters of these species, we selected three widely separated sites in shrubsteppe habitat in the northern Great Basin: Arid Lands Ecology Reserve (ALE) in southeastern Washington, Cabin Lake in central Oregon, and Star Creek in northern Nevada (Fig. 1). Although these sampling sites span a latitudinal gradient of over 650 km and the vegetation at each differs in its details from that at the others, the sites nonetheless are generally similar (Table 1) and each includes large tracts of sagebrush-dominated habitat. We spent several weeks at each of these sites during the breeding seasons of 1976 and 1977 (Table 1). Details of the measurements of bird densities and vegetation attributes may be found in Wiens et al. (1987).

To assess the temporal components of variation in reproductive parameters, we studied populations at a single site, the centrally located Cabin Lake, for five consecutive years (1976–1980). In addition to measuring reproductive parameters, we monitored bird population densities on the two 9-ha plots on which most of the nests were found. We also recorded annual and "bioyear" (October through April) precipitation from a standard NOAA weather station (Fremont, Oregon) approximately 15 km distant. Because of

TABLE 2. Sample sizes of nests stratified by year and site. Entries are number of nests of Sage Sparrows/Brewer's Sparrows/Sage Thrashers.

| Site | Year | | | | | Total (temporal) |
	1976	1977	1978	1979	1980	
ALE	22/—/—[a]	7/—/—				
Cabin Lake	9/20/3	10/26/4	9/16/8	15/37/8	9/11/8	52/110/31
Star Creek	8/—/1	9/12/1				
Total (geographical)	65/58/9					

[a] — denotes species absent from site.

the type of vegetation and temperature/precipitation patterns in the northern Great Basin, precipitation occurring during the bioyear is more relevant to biological production during the subsequent spring and summer (Daubenmire 1970, Thorp and Hinds 1977) than is total annual precipitation, which is accumulated over the preceding calendar year (e.g., Rosenzweig 1968).

At each site we located as many nests as possible. Most were found during the incubation stage. Each nest was visited daily until either the chicks fledged, nest contents were preyed upon, or we left the site. In quantifying clutch size we assumed that each nest contained a completed clutch. Because some nests potentially may have suffered partial egg losses before they were discovered, this procedure underestimates true clutch size. However, in our data this bias is likely to be small; in 1,040 nest days of observations on nests with eggs (all species, all sites, all years), we observed only two instances of partial clutch loss.

We assumed that a nest was lost to predation by applying the conventional criterion (Ricklefs 1969): the sudden disappearance of eggs or of otherwise apparently healthy chicks. Because we visited nests and weighed chicks daily, we can be fairly confident of our assessment of causes of nest failure. Although we have no independent data that allow us to assess the effects of frequent nest visitation on success or predation rates (Gottfried and Thompson 1978, Westmoreland and Best 1985), there were no obvious manifestations of observer effects. As visitation frequency was consistent among sites and years, the comparisons made below should be valid.

STATISTICAL ANALYSIS

For the geographical analysis, differences among means of reproductive parameters for Sage Sparrows were analyzed using nested ANOVA, with site as the main effect and year as a random variable nested within site. Although year has the same "value" across all sites, it is treated as a random effect in this model because, first, it represents a random sample of years over which we wish to generalize, and, second, its inclusion as a random-effects nested factor will account for some within-site variability and thereby make hypothesis testing for the fixed effect (site) of primary importance. Thus, the appropriate test of differences among sites is the ratio of the site mean square to the year-within-site mean square (Zar 1984:256); this provides a test for significant variation among sites over and above any variation between years. This model was inappropriate for Brewer's Sparrows and Sage Thrashers, however, because of an extremely unbalanced design (see Table 2). Geographical variation in these species was tested using one-way ANOVA with site as the main effect, and pooling years. For all species only Cabin Lake data from 1976–1977 were used in geographical comparisons. For the temporal analysis, differences among all years at Cabin Lake were analyzed using one-way ANOVA with year as the main effect. Type III sums of squares, which adjust for unequal sample sizes within ANOVA classes, were used. Because variances were homoscedastic, all statistical tests were performed on untransformed variables. Duncan's multiple range test was used for a posteriori comparisons of means. All ANOVAs were performed using Statistical Analysis System PROC GLM (SAS Institute 1982). The statistical significance of correlations between reproductive parameters and precipitation was assessed using methods outlined in Zar (1984:278) appropriate for multiple observations of one variable for each value of a second variable (i.e., several nests per year).

Because nests were discovered at different times in the nesting cycle and in the season, and because nests were observed for differing periods (some were still active when we left a site), we used the method of Hensler and Nichols (1981) to estimate average daily nest-survival rates, their standard deviations, and probability of nest success (Mayfield 1975). Differences in nest-survival rates among sites and among years were tested by one-way ANOVA using means and variances (Zar 1984:168). Because Hensler and Nichols' equation for estimating variance is discontinuous for samples in which all nests were successful, we added an artificial datum of one unsuccessful nest observed for 1 day to such samples in our data set, and used the resulting variance estimate (but not its increased sample size) in our ANOVAs.

RESULTS

We examined 33 Sage Thrasher, 98 Sage Sparrow, and 122 Brewer's Sparrow nests (Table 2). Not all nests were available for all analyses, however, because of missing values for some variables (e.g., although a nest was known to contain three eggs, the number of chicks produced might be unknown because we left the site before the eggs hatched). Thrashers and Brewer's Sparrows were absent from ALE, the northernmost site, during the 2 years of our data collection, although they occurred there sporadically in other years (Rotenberry and Wiens, pers. observ.). Brewer's Sparrows were absent from Star Creek during 1 year of our study.

GEOGRAPHICAL ANALYSIS

For Sage and Brewer's sparrows, the mean clutch size did not differ significantly ($P > 0.10$) between sites (Fig. 2). Grand means were 3.06 ± 0.06 (53) [mean ± SE (n)] for Sage and 3.04 ± 0.08 (50) for Brewer's sparrows; about 70% of the nests of both species contained three eggs. Sage Thrashers were omitted from this analysis due to the small sample size at Star Creek (but see below).

Translation of these rather uniform clutch sizes into subsequent chicks, however, was clearly not the same across sites; brood sizes at Star Creek were substantially lower ($P < 0.01$) for both species than at the other sites (Fig. 2). This difference in the mean number of chicks was propagated as a significant difference among sites in the average number of fledglings for Brewer's
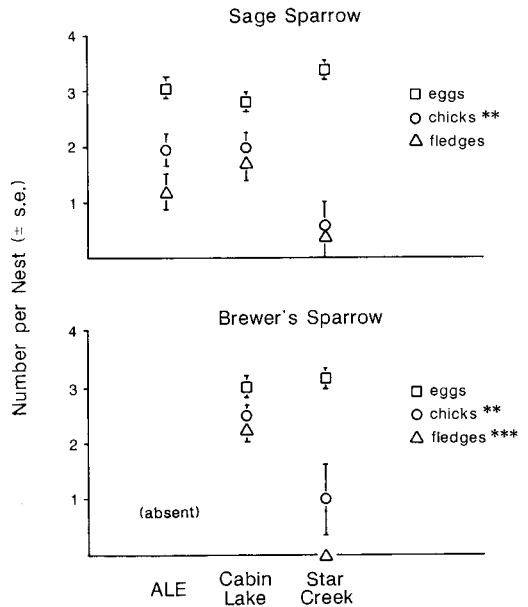

FIGURE 2. Average number of eggs, chicks, and fledglings produced by two species of shrubsteppe passerines at three sites. * denotes statistically significant among-site variation (** = $P < 0.01$, *** = $P < 0.001$; ANOVA). Sample sizes for Sage Sparrows range from 19–23 at ALE, 11–16 at Cabin Lake, and 10–14 at Star Creek; for Brewer's Sparrows, 35–38 at Cabin Lake, 5–12 at Star Creek.

Sparrows ($P < 0.001$). Indeed, for all the nests for which we knew the final outcome, Brewer's Sparrows at Star Creek failed to produce any fledglings. Brood-size differences among sites for Sage Sparrows, on the other hand, failed to generate statistically significant among-site variation in number of fledglings ($P > 0.10$).

The reason for these results became evident when we examined nest-survivorship probabilities and the proportion of nests at a site that were lost to predation (Table 3). Only 11% of the Brewer's Sparrow nests at Cabin Lake were lost to predators during 1976–1977, whereas all of those at Star Creek (1977 only) were. Although the Star Creek sample was small, it was statistically highly unlikely ($P < 0.001$) that these two sites shared the same predation rate. Likewise, there was highly significant among-site heterogeneity in nest survivorship and predation rates on Sage Sparrow nests. Predation rate was high at Star Creek, intermediate at ALE, and nil at Cabin Lake.

We can expand the scope of our geographical

TABLE 3.   Geographical variation in nest survival and predation rates, 1976–1977. Entries are predation nests/successful nests, daily survival rate (p) ± SD[a], and probability of nest success.[b]

Species	Predation rate			P-value[c]
	ALE	Cabin Lake	Star Creek	
Sage Sparrow	6/9	0/11	10/1	
	0.96 ± 0.02	1.00 ± 0.01	0.75 ± 0.07	<0.001
	0.39	1.00	0.001	
Brewer's Sparrow	—	4/31	4/0	
		0.99 ± 0.01	0.81 ± 0.09	<0.001
		0.85	0.01	
Combined nests	6/9	4/42	14/1	

[a] p estimated using method of Hensler and Nichols (1981); SD estimated using method of Hensler and Nichols (1981) except where p = 1.00 (see text for details).
[b] p^j, where j is nesting period. j = 24 days for Sage Sparrows, 21 days for Brewer's Sparrows (Petersen and Best 1987), 27 days for Sage Thrashers (Reynolds and Rich 1978).
[c] ANOVA test of Ho: nest survival rate is independent of site.

analyses by comparing our observations to those of Reynolds (1981) for these same three species in similar sagebrush-dominated habitat in southeastern Idaho (Fig. 1, INEL site). For Sage Thrashers (the most numerous species in Reynolds' sample), there were no significant differences in the number of eggs, chicks (Reynolds included only those nests surviving to hatching), or fledglings per nest between INEL and Cabin Lake (t'-test [Zar 1984:131], all P > 0.10). For Brewer's Sparrows, there were significantly more fledglings per nest at Cabin Lake than at INEL (2.5 vs. 0.5, P < 0.05); other attributes did not differ significantly. The low number of fledglings at INEL was due to high nest-predation rates; only one of seven nests successfully fledged young. For Sage Sparrows, sample sizes were sufficient to compare all three of our sites to Idaho; the only attribute that differed significantly was the number of eggs per nest at Star Creek, which averaged 0.6 higher than at INEL (3.4 vs. 2.8, P < 0.05).

TEMPORAL ANALYSIS

Different patterns of variation were observed when we shifted our focus from several sites sampled in the same years to a single site, Cabin Lake, sampled over a longer period (Fig. 3). There was statistically significant variation in virtually all of the reproductive parameters measured. As assessed by one-way analysis of variance, the average number of eggs, chicks, and fledglings each had a significant component of annual variation in both sparrow species (all P < 0.05), and the number of eggs varied significantly (P < 0.01) in thrashers. Statistically, "year" accounted for 12–45% of the total variation in these attributes.

During the 5 years over which our observations were made, the northern Great Basin experienced extremes in precipitation, with the driest bioyear in 65 years of records (1976–1977; Thorp and Hinds 1977) followed by one of the wettest (1977–1978; Fig. 4A), and several components of bird reproductive parameters were significantly correlated with this variation (Table 4). In Brewer's Sparrows, all three reproductive components increased with increasing precipitation the preceding bioyear, especially clutch size. For Sage Sparrows, only brood size was significantly correlated with rainfall, although the number of fledglings produced appeared marginal (P = 0.06, Table 4). No components of Sage Thrashers approached statistical significance, and, although there were relatively few nests for this species (hence the power of our tests was low), the magnitude of the correlation coefficients suggests that any effect, if present, was very slight.

Some reproductive attributes were also significantly correlated with bird population densities: the average number of chicks and fledglings produced by Sage Sparrows was negatively associated with the average density of Brewer's Sparrows (both r = −0.87, P = 0.05), and the number of eggs laid by thrashers was positively correlated with the total density of all bird species (r = 0.89, P = 0.04).

As before, there emerged a clear pattern of variation associated with predation. Rates of nest survival and predation were not uniform across years (Table 5), reaching a peak for all species in 1979. In 1979, clutch sizes of Sage Sparrows and Sage Thrashers were relatively large, but relatively small numbers of chicks and fledglings were produced (Fig. 3). To a lesser extent, the same
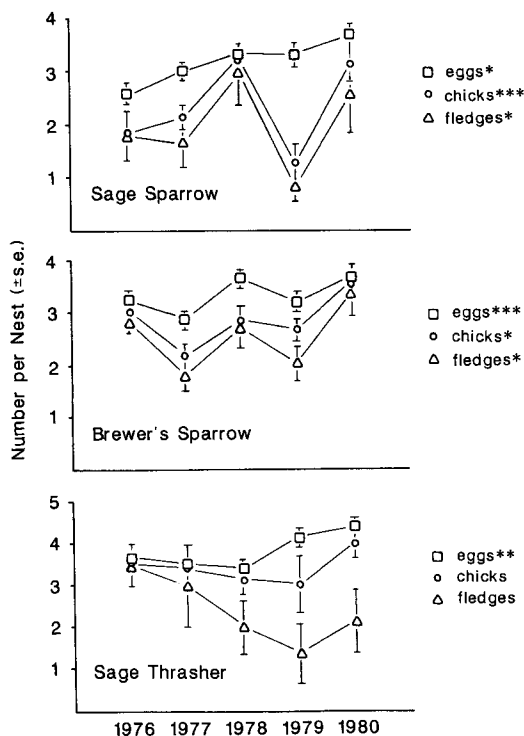
FIGURE 3. Average number of eggs, chicks, and fledglings produced by three species of shrubsteppe passerines at Cabin Lake over 5 years. * denotes statistically significant among-year variation (* = $P <$ 0.05, ** = $P < 0.01$, *** = $P < 0.001$; ANOVA). See Table 2 for approximate sample sizes.

FIGURE 4. Variation in precipitation and bird population densities recorded at Cabin Lake over 5 years. A. Total (January–December) and bioyear (October–April) precipitation accumulated over calendar year preceding bird censuses. B. Bird densities averaged from censuses taken on two replicate plots.

pattern was observed for Brewer's Sparrows (Fig. 3).

We can also compare our temporal observations to similar ones made over a 5-year period (1980–1984) at INEL by Petersen and Best (1987). However, the presentation of their da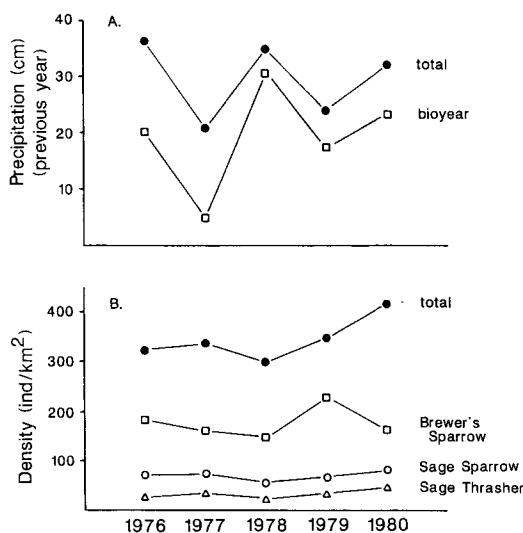ta (which reflects the different goal of their study, to compare breeding biology on burned vs. unburned plots) precludes direct statistical comparison with ours. On control (i.e., unburned) plots they noted significant annual variation in Sage Sparrow clutch sizes, the average number of young fledging from successful nests, and daily survival probabilities. None of these attributes varied significantly in Brewer's Sparrows on control plots.

CLUTCH SIZE AND REPRODUCTIVE SUCCESS

Predation appeared to have profound effects on the translation of clutch size to fledged young at both geographical and temporal scales of analysis. In tracing the fate of clutches of three and

TABLE 4. Correlations between bird reproductive parameters and precipitation during the preceding bioyear, Cabin Lake, 1976–1977. Sample sizes in parentheses. * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

Species	Reproductive parameter		
	Eggs	Chicks	Fledglings
Sage Sparrow	0.18 (44)	0.34* (46)	0.31 (39)
Brewer's Sparrow	0.45*** (93)	0.26** (95)	0.28** (81)
Sage Thrasher	−0.08 (30)	−0.02 (30)	−0.05 (26)

TABLE 5. Temporal variation in nest survival and predation rates at Cabin Lake, 1976–1980. Entries are predation nests/successful nests, daily survival rate (p) ± SD[a], and probability of nest success[b].

| Species | Predation rate | | | | | P-value[c] |
	1976	1977	1978	1979	1980	
Sage Sparrow	0/4	0/7	1/5	7/6	1/5	
	1.00 ± 0.02	1.00 ± 0.01	0.98 ± 0.02	0.93 ± 0.03	0.99 ± 0.01	<0.001
	1.00	1.00	0.66	0.17	0.73	
Brewer's Sparrow	0/16	4/15	0/9	7/19	0/8	
	1.00 ± 0.01	0.99 ± 0.01	1.00 ± 0.01	0.98 ± 0.01	1.00 ± 0.01	<0.001
	1.00	0.78	1.00	0.61	1.00	
Sage Thrasher	0/2	0/2	2/4	4/3	2/6	
	1.00 ± 0.04	1.00 ± 0.02	0.98 ± 0.01	0.96 ± 0.02	0.98 ± 0.01	>0.10
	1.00	1.00	0.61	0.31	0.61	
Combined	0/22	4/24	3/18	18/28	3/19	

[a] p estimated using method of Hensler and Nichols (1981); SD estimated using method of Hensler and Nichols (1981) except where $p = 1.00$ (see text for details).
[b] p^j, where j is nesting period. $j = 24$ days for Sage Sparrows, 21 days for Brewer's Sparrows (Peterson and Best 1987), 27 days for Sage Thrashers (Reynolds and Rich 1978).
[c] ANOVA test of Ho: nest survival rate is independent of site.

four eggs in Sage Sparrows at ALE and Star Creek, for example, we found no significant difference in the numbers of offspring fledged from the two clutch sizes (one-way ANOVA, $P > 0.90$). Much of this mortality occurred during the egg stage, although some obviously persisted during the nestling period (Fig. 5A). Likewise, the number of chicks fledged from clutches of three and four at Cabin Lake during the high-predation year 1979 did not differ significantly ($P > 0.30$; Fig. 5B). This is not due to the inability of parents to care for more than one chick; brood reduction was rare (we observed one instance in 5 years at Cabin Lake) and, if they are undisturbed by predators, Sage Sparrows routinely rear three or four healthy young. Excluding data from 1979, 69% of the Sage Sparrow nests at Cabin Lake that contained three or four eggs produced three or four fledglings, and in one experimentally augmented nest a pair successfully reared five chicks to fledging. In the absence of heavy predation, clutches of different sizes produced significantly different numbers of fledglings ($P < 0.01$; Fig. 5C). Over all 5 years combined, however, the correlation between clutch size and number of fledglings produced was not significant ($r = 0.21$, $P = 0.26$, 32 nests).

The overall linkage between clutch size and number of fledglings was stronger in Brewer's Sparrows ($r = 0.33$, $P = 0.01$, 64 nests), despite the observation that in 1979 there was no significant difference between clutch size and number of fledglings ($P = 0.35$, Fig. 6B). When data from 1979 are excluded (Fig. 6A), nests that

started out with either three or four eggs produced, on average, significantly more fledglings than did two-egg nests ($P < 0.001$), although they did not differ significantly between themselves. The lack of difference in fledgling production between three- and four-egg nests is primarily due to the lower average hatching success of the latter (Fig. 6A).

In thrashers (Fig. 7), as with Sage Sparrows, there was no overall correlation between initial clutch size and final nest productivity ($r = 0.12$, $P = 0.57$, 25 nests). Although the average number of fledglings produced from clutches of three, four, and five eggs did not differ ($P > 0.05$), the average number of chicks did ($P < 0.001$). This reflects the fact that most predation on thrasher nests occurred on chicks rather than eggs; only one of 29 thrasher nests at Cabin Lake experienced egg loss. Reynolds and Rich (1978) also observed significantly greater nestling loss than egg loss by Sage Thrashers in southeastern Idaho.

Skutch (1949) suggested that the probability of nest predation increases as the number of chicks in the nest increases. This relationship is presumed to be a consequence of the greater conspicuousness of nests containing more chicks because of increased noise levels of chicks and/or increased frequency of nest visits by parents feeding young. In Brewer's Sparrows, 63 successful nests averaged 3.0 ± 0.91 chicks, whereas five nests that incurred losses of chicks averaged 2.8 ± 0.45, opposite to the direction predicted by Skutch. In Sage Thrashers, similar statistics were 3.7 ± 0.85 for 17 successful nests and 3.8 ± 0.75
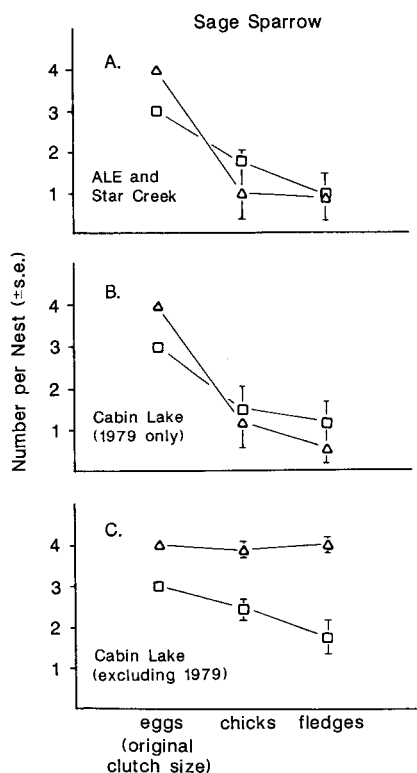
FIGURE 5.   Average number of chicks and fledglings produced by Sage Sparrows from clutches of different initial sizes. A. ALE and Star Creek, 1976–1977 (high predation sites; $n = 9, 27$). B. Cabin Lake, 1979 only (high predation year; $n = 6, 6$). C. Cabin Lake, 1976–1978, 1980 (low predation years; $n = 7, 24$).
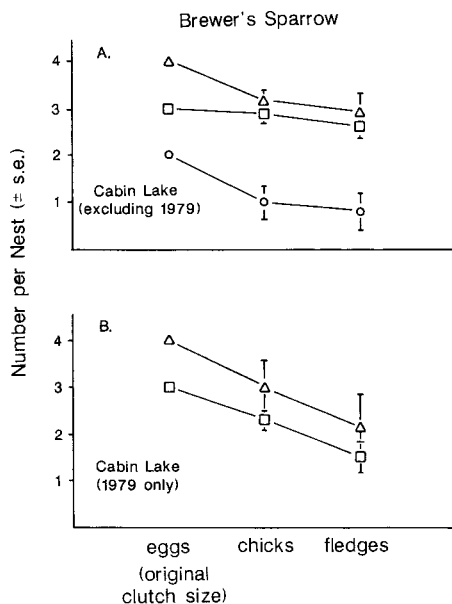

FIGURE 6.   Average number of chicks and fledglings produced by Brewer's Sparrows from clutches of different initial sizes. A. Cabin Lake, 1976–1978, 1980 (low predation years; $n = 22, 32, 7$). B. Cabin Lake, 1979 only (high predation year; $n = 7, 24$).

for six unsuccessful ones. Although our sample sizes are relatively small, these data provide little support for clutch size-dependent predation in these species.

DISCUSSION

Our data clearly show that predation plays a major role in affecting the reproductive success of passerine birds in shrubsteppe habitat. Moreover, the type of predator and intensity of predation are variable in both geographical and temporal contexts. This variation is likely to have important consequences for the evolution of reproductive parameters in these species.

VARIATION IN PREDATORS AND
PREDATION RATE

We believe that the principal nest predators at ALE and Star Creek are snakes, particularly go-

pher snakes (*Pituophis melanoleucus*: Colubridae), which are quite abundant at these two sites. Most of our evidence implicating snakes is indirect; usually the nest contents had disappeared but the physical structure of the nest remained undisturbed. On two occasions, however, we found nests at Star Creek with small gopher snakes still in them (and the contents of the nest quite
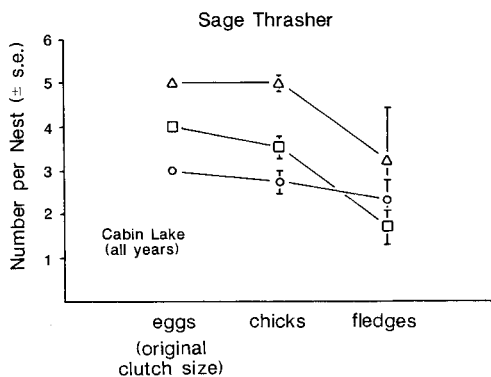

FIGURE 7.   Average number of chicks and fledglings produced by Sage Thrashers from clutches of different initial sizes, Cabin Lake, 1976–1980 ($n = 4, 18, 8$).

evidently still in the snake), and where we used time-lapse movie cameras to monitor adult bird behavior at nests, we recorded snakes taking chicks in two instances. Finally, at Cabin Lake, where nest losses to predation were virtually nil during 1976–1977 (Tables 3, 5), snakes of all species are absent (Rotenberry, Wiens, and others, pers. observ. based on thousands of person-hours in the field at Cabin Lake and the surrounding Fort Rock Basin between 1975–1983).

Even in the absence of snakes, there were several potential nest predators at Cabin Lake (e.g., Common Ravens [Corvus corax: Corvidae], long-tailed weasels [Mustela frenata: Mustelidae], chipmunks [Eutamias spp.: Sciuridae]). Unlike Reynolds (1979), we do not believe that Loggerhead Shrikes (Lanius ludovicianus: Laniidae) played an important role either in affecting nest success in the populations we observed or in producing the patterns of differences in predation rates among sites. The patterns of chick loss that we observed (in most cases all chicks disappearing simultaneously) differed from that described by Reynolds for shrike predation (disappearance of one or two chicks per day per nest until all were gone). In addition, a substantial proportion of the nest predation we observed occurred during the egg stage. Finally, shrikes occurred in more or less equal (very low) abundances at all three of our sites. We believe that the principal predators during 1979 at Cabin Lake were Townsend's ground squirrels (Spermophilus townsendi: Sciuridae). In many of the nests suffering predation in 1979, the nest lining was ripped out and, in some cases, the entire nest cup had been pulled out of the nest shrub, suggesting mammalian predation. Petersen and Best (1987) also implicated S. townsendi, as well as chipmunks, as the principal nest predators at their site.

Although Spermophilus are "ground" squirrels, they readily climb sagebrush (Rotenberry and Wiens, pers. observ.) and thus attain easy access to nests. Although they are primarily herbivorous, squirrels of this genus and species (especially juvenile males) are known to be facultatively carnivorous (Alcorn 1940, Sherman 1982). Like many other rodent species, ground squirrels undergo population fluctuations during which their densities may vary over several orders of magnitude in just a few years, and at least in this species such fluctuations may be driven by climatic variation (Smith and Johnson 1985).

Abundances of ground squirrels appeared to be exceptionally high on our bird study plots at Cabin Lake in 1979. This pattern probably reflects the recovery of the local population following the drought of 1976–1977. If we assume that the demography of S. townsendi at Cabin Lake parallels that documented for the same species in similar habitat in southwestern Idaho during the same period (1975–1981; Smith and Johnson 1985), then the following scenario seems likely. Low precipitation during the bioyear 1976–1977 led to reduced overwinter survival of adults (21% in southwestern Idaho) and, because of the absence of sufficient green forage in the spring, no reproduction occurred in 1977. Thus, few adults and no yearlings emerged in 1978. But because an exceptionally wet bioyear in 1977–1978 produced considerable green vegetation, per capita reproductive output was high (significantly higher in 1978 than all other years, 1975–1981; Smith and Johnson 1985). Following another adequate bioyear of precipitation in 1978–1979, which led to good overwinter survival and abundant spring forage, both adults and yearlings emerged in 1979 in high numbers and produced large litters, which led to the abundance of predatory juveniles. Although the 1979–1980 bioyear was relatively wet, the number of squirrels active on our bird plots in 1980 appeared to be much reduced from that in 1979, as were squirrel populations in Idaho (Smith and Johnson 1985), perhaps due to dispersal, predation, or disease. Thus, the general pattern of ground squirrel demography, coupled with the extreme year-to-year variation in precipitation observed in this region, is consistent with the apparently episodic nature of relatively intense predation observed at Cabin Lake.

REPRODUCTIVE SUCCESS AND PRECIPITATION

The simplest view of the relationship between avian reproductive success and precipitation in arid environments is that high precipitation drives increased primary production (e.g., Went 1955, Rosenzweig 1968), which in turn promotes increased secondary production (i.e., increased biomass of insects and other important invertebrate prey; e.g., Seely and Louw 1980, Cody 1981, Fuentes and Campusano 1985), which is then translated into increased clutch sizes and/or fledging success (e.g., Immelmann 1971, Serventy 1971). Although such patterns have been observed in relatively predator-free arid envi-

ronments (e.g., Boag and Grant 1984), our data suggest that the relationship between avian reproductive success and precipitation in shrubsteppe regions may be more complex. This complexity arises from the effect of increased production on populations of potential predators. Data from Smith and Johnson (1985) and our own observations suggest that ground squirrels responded to increased precipitation, but did so (from the point of view of reaching densities sufficient to affect bird nesting success) with a 2-year lag. This apparent lag in the response of a predator population creates a more complex, higher-order relationship between precipitation and shrubsteppe bird reproductive success. Further, Smith and Johnson (1985) point out that ground squirrels serve as an important prey for other predators, such as gopher snakes, weasels, and ravens, creating still other indirect links between climate and bird reproduction.

The strongest association between rainfall and bird reproductive parameters involved the significant positive correlation between clutch size in Brewer's Sparrow and bioyear precipitation (Table 4). Taken at face value, it suggests that Brewer's Sparrows are able to increase their initial reproductive investment in accordance with potentially favorable environmental conditions. Of all the common shrubsteppe bird species, Brewer's Sparrows seem most likely to be able to respond to local conditions in an opportunistic fashion. Their abundances vary considerably from year to year at individual plots and their densities display the highest coefficient of variation (Rotenberry and Wiens 1980, Wiens et al. 1987). Indeed, they were completely absent from Star Creek in 1976, only to be present in relatively high abundance in 1977 (Tables 1, 2). It also seems evident that, despite episodic predation at Cabin Lake, relatively high clutch sizes during more productive (i.e., wetter) years translates into relatively greater final reproductive success (Table 4, Fig. 6).

Although Sage Sparrow clutch sizes were not correlated with increasing bioyear precipitation, the average number of chicks hatched was. Thus, Sage Sparrows appear to respond to increased productivity not by increasing the number of eggs laid, but by increasing their quality (i.e., hatchability). Although the negative correlation between the number of chicks and fledglings produced by Sage Sparrows and the average density of Brewer's Sparrows seems suggestive of an intense interspecific interaction, we are inclined to discount it as spurious. The association appears to arise because of the coincidence of peak abundance of Brewer's Sparrows in 1979 (Fig. 4) with peak predation on Sage Sparrow nests during the same year (Table 5), two events that appear biologically unrelated. If competition were important in reducing Sage Sparrow reproductive output, we would expect to see the effect of starvation (slow growth rates, gradual disappearance of nestlings, low weights at fledging), which differ considerably from those attributed to predation (see above) and which we did not observe (Rotenberry and Wiens, unpubl.).

Factors responsible for the positive correlation between Sage Thrasher clutch size and total avian density were not apparent. Others have noted an association between breeding density and clutch size (e.g., Goossen and Sealy 1982, Blancher and Robertson 1985) and attributed such a relationship to the covariation of clutch size and density with food abundance. However, breeding bird density and precipitation (and, presumably, primary and secondary production) were not correlated ($r = -0.09$, $P > 0.80$), in contrast to patterns reported by Cody (1981) and Smith (1982). Although it is possible that productivity of bird food did not vary in concert with precipitation, such seems unlikely for three reasons: (1) a pattern of correlation between primary and secondary production and precipitation is common in arid regions (e.g., Seely and Louw 1980, Cody 1981, Fuentes and Campusano 1985), and such a correlation was observed for primary production in the northern Great Basin during 1977–1979 (Rotenberry and Wiens 1980); (2) precipitation varied over an extreme range during our study period; and (3) reproductive parameters of Sage and Brewer's sparrows appeared to respond in a manner consistent with a productivity/precipitation linkage.

In summary, all three of the species we considered demonstrated a substantial amount of geographical and annual variation in several relevant reproductive parameters. Moreover, the species experienced considerable spatial and temporal variation in predation, a phenomenon observed in a variety of temperate zone passerines (e.g., Murphy 1978, Goossen and Sealy 1982, Murphy 1983, Petrinovich and Patterson 1983, Blancher and Robertson 1985). When nest predation on a species differs among areas and years, it can influence life-history traits, habitat use,

and community patterns (Slagsvold 1982, 1984; Martin, in press). In this context, it is important to note that both the rate of predation and the type of predator vary. The nesting strategies that reduce the probability of predation by snakes likely differ considerably from those that may minimize the probability of predation by ground squirrels (Martin 1987). Likewise, the effects of predation that occur more or less continually or predictably will likely select for a different suite of adaptive responses than predation that is unpredictably episodic. Certainly predation has shaped some components of these birds' behavior; nests of all three species are cryptic and distributed nonrandomly within the vegetation, being placed in relatively denser microhabitats where they are presumably less obvious and less accessible to predators (Rich 1978; Petersen and Best 1985a, 1985b).

Further, spatiotemporally episodic predation is likely to exert a strong effect on patterns of recruitment of individuals into breeding populations. Because intense predation by small mammals may occur out of phase or lagged with respect to resource fluctuations, it may operate to decouple variation in bird population abundances from variation in resource abundances, thus accounting for the apparent lack of avian community "organization" that we have noted before in this ecosystem (e.g., Rotenberry 1980, Wiens and Rotenberry 1981). However, because the details of the linkage between nest predation and adult recruitment in populations of nonphilopatric migratory birds are unknown, the effectiveness of this proposed decoupling mechanism remains highly speculative.

As with many studies of this sort, more questions are raised than are answered. Why do Sage and Brewer's sparrows, birds of dissimilar size, energetics, abundance, habitat distribution, phylogeny, and other components of ecology and life history, have virtually identical clutch sizes? What mechanism(s) is responsible for the apparent buffering of Sage Thrasher reproductive output from the extremes of climatic variation we observed? Does nest predation influence avian community structure, as has been suggested for bird assemblages in physiognomically more complex habitats (Martin, in press)? Although we currently lack the data to resolve these questions, we think it is clear that questions of this sort, involving the simultaneous consideration of variation in reproductive parameters in time and space, should be high on the ecologist's agenda.

LITERATURE CITED

ALCORN, J. R. 1940. Life history notes on the Piute ground squirrel. J. Mammal. 21:160–170.

BENT, A. C. 1948. Life histories of North American nuthatches, wrens, thrashers, and their allies. U.S. Natl. Mus. Bull. 195.

BLANCHER, P. J., AND R. J. ROBERTSON. 1985. Site consistency in kingbird breeding performance: implications for site fidelity. J. Anim. Ecol. 54:1017–1027.

BOAG, P. T., AND P. R. GRANT. 1984. Darwin's finches (Geospiza) on Isla Daphne Major, Galapagos: breeding and feeding ecology in a climatically variable environment. Ecol. Monogr. 54:463–489.

BRAUN, C. E., M. F. BAKER, R. L. ENG, J. S. GASHWILER, AND M. H. SCHROEDER. 1976. Conservation committee report on effects of alteration of sagebrush communities on the associated avifauna. Wilson Bull. 88:165–171.

CODY, M. L. 1981. Habitat selection in birds: the roles of vegetation structure, competition, and productivity. Bioscience 31:107–113.

DAUBENMIRE, R. 1970. Steppe vegetation of Washington. Tech. Bull. 62, Washington Agricultural Experiment Station, Pullman, WA.

FEIST, F. G. 1968. Breeding-bird populations on sagebrush-grassland habitat in central Montana. Audubon Field Notes 22:691–695.

FRANKLIN, J. F., AND C. T. DYRNESS. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-8, Portland, OR.

FUENTES, E. R., AND C. CAMPUSANO. 1985. Pest outbreaks and rainfall in the semi-arid region of Chile. J. Arid Environ. 8:67–72.

GOOSSEN, J. P., AND S. G. SEALY. 1982. Production of young in a dense nesting population of Yellow Warblers, Dendroica petechia, in Manitoba. Can. Field-Nat. 96:189–199.

GOTTFRIED, B. M., AND C. F. THOMPSON. 1978. Experimental analysis of nest predation in an old-field habitat. Auk 95:304–312.

HENSLER, G. L., AND J. D. NICHOLS. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bull. 93:42–53.

IMMELMANN, K. 1971. Ecological aspects of periodic reproduction, p. 341–389. In D. S. Farner and J.

R. King [eds.], Avian biology. Vol. 1. Academic Press, New York.

KLOMP, H. 1970. The determination of clutch size in birds. A review. Ardea 58:1–124.

LACK, D. 1943. The life of the Robin. H. F. and G. Whitherby, London, England.

MARTIN, T. E. 1987. Artificial nest experiments: effects of nest appearance and type of predator. Condor 89:925–928.

MARTIN, T. E. In press. Processes organizing open-nesting bird assemblages: competition or nest predation? Evol. Ecol.

MAYFIELD, H. 1975. Suggestions for calculating nest success. Wilson Bull. 87:456–466.

MILLER, A. H. 1968. Northern Sage Sparrow, p. 1004–1013. In A. C. Bent [ed.], Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237.

MURPHY, E. C. 1978. Breeding ecology of House Sparrows: spatial variation. Condor 80:180–193.

MURPHY, M. T. 1983. Nest success and nesting habits of Eastern Kingbirds and other flycatchers. Condor 85:208–219.

NOLAN, V. 1978. The ecology and behavior of the Prairie Warbler, Dendroica discolor. Ornithol. Monogr. No. 26. American Ornithologists' Union, Washington, DC.

PAINE, R. T. 1968. Brewer's Sparrow, p. 1208–1217. In A. C. Bent [ed.], Life histories of North American cardinals, grosbeaks, buntings, towhees, finches, sparrows, and allies. U.S. Natl. Mus. Bull. 237.

PETERSEN, K. L., AND L. B. BEST. 1985a. Nest-site selection by Sage Sparrows. Condor 87:217–221.

PETERSEN, K. L., AND L. B. BEST. 1985b. Brewer's Sparrow nest-site characteristics in a sagebrush community. J. Field Ornithol. 56:23–27.

PETERSEN, K. L., AND L. B. BEST. 1986. Diets of nestling Sage Sparrows and Brewer's Sparrows in an Idaho sagebrush community. J. Field Ornithol. 57: 283–294.

PETERSEN, K. L., AND L. B. BEST. 1987. Effects of prescribed burning on nongame birds in a sagebrush community. Wildl. Soc. Bull. 15:317–329.

PETRINOVICH, L., AND T. L. PATTERSON. 1983. The White-crowned Sparrow: reproductive success (1975–1980). Auk 100:811–825.

REYNOLDS, T. D. 1979. Impact of Loggerhead Shrikes on nesting birds in a sagebrush environment. Auk 96:798–800.

REYNOLDS, T. D. 1981. Nesting of the Sage Thrasher, Sage Sparrow, and Brewer's Sparrow in southeastern Idaho. Condor 83:61–64.

REYNOLDS, T. D., AND T. D. RICH. 1978. Reproductive ecology of the Sage Thrasher (Oreoscoptes montanus) on the Snake River Plain in south-central Idaho. Auk 95:580–582.

RICH, T. D. 1978. Nest placement in Sage Thrashers. Wilson Bull. 90:303.

RICH, T. D. 1980. Nest placement in Sage Thrashers, Sage Sparrows and Brewer's Sparrows. Wilson Bull. 92:362–368.

RICKLEFS, R. E. 1969. An analysis of nesting mortality in birds. Smithson. Contrib. Zool. 9:1–48.

ROSENZWEIG, M. L. 1968. Net primary productivity of terrestrial communities: prediction from climatological data. Am. Nat. 102:67–74.

ROTENBERRY, J. T. 1980. Dietary relationships among shrubsteppe passerine birds: competition or opportunism in a variable environment? Ecol. Monogr. 50:93–110.

ROTENBERRY, J. T., AND J. A. WIENS. 1978. Nongame bird communities in northwestern rangelands, p. 32–46. In R. M. DeGraaf [ed.], Proceedings of a workshop on nongame bird habitat management in coniferous forests of western United States. USDA For. Serv. Gen. Tech. Rep. PNW-64, Pacific Northwest Forest and Range Experiment Station, Portland, OR.

ROTENBERRY, J. T., AND J. A. WIENS. 1980. Temporal variation in habitat structure and shrubsteppe bird dynamics. Oecologia (Berl.) 47:1–9.

RYSER, F. A. 1985. Birds of the Great Basin. Univ. of Nevada Press, Reno.

SAS INSTITUTE. 1982. SAS user's guide: statistics. SAS Institute, Cary, NC.

SEELY, M. K., AND G. N. LOUW. 1980. First approximation of the effects of rainfall on the ecology and energetics of a Namib Desert dune ecosystem. J. Arid Environ. 3:25–54.

SERVENTY, D. L. 1971. Biology of desert birds, p. 287–339. In D. S. Farner and J. R. King [eds.], Avian biology. Vol. 1. Academic Press, New York.

SHERMAN, P. W. 1982. Infanticide in ground squirrels. Anim. Behav. 30:938–939.

SKUTCH, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis 91:430–455.

SLAGSVOLD, T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. Oecologia (Berl.) 54:159–169.

SLAGSVOLD, T. 1984. Clutch size variation of birds in relation to nest predation: on the cost of reproduction. J. Anim. Ecol. 53:945–953.

SMITH, G. W., AND D. R. JOHNSON. 1985. Demography of a Townsend ground squirrel population in southwestern Idaho. Ecology 66:171–178.

SMITH, K. G. 1982. Drought-induced changes in avian community structure along a montane sere. Ecology 63:952–961.

THORP, J. M., AND W. T. HINDS. 1977. Microclimates of the Arid Lands Ecology Reserve, 1968–1975. BNWL-SA-6231, Battelle Pacific Northwest Laboratories, Richland, WA.

VERNER, J. 1965. Breeding biology of the Long-billed Marsh Wren. Condor 67:6–30.

WAGNER, H. O. 1957. Variation in clutch size at different latitudes. Auk 74:243–250.

WENT, F. W. 1955. The ecology of desert plants. Sci. Am. 192:68–75.

WEST, N. E. [ED.]. 1983. Ecosystems of the world—5. Temperate deserts and semi-deserts. Elsevier Scientific Publications, New York.

WESTMORELAND, D., AND L. B. BEST. 1985. The effect of disturbance on Mourning Dove nesting success. Auk 102:774–780.

WIENS, J. A. 1974. Climatic instability and the "ecological saturation" of bird communities in North American grasslands. Condor 76:385–400.

WIENS, J. A., AND J. T. ROTENBERRY. 1979. Diet niche

relationships among North American grassland and shrubsteppe birds. Oecologia (Berl.) 42:253–292.

WIENS, J. A., AND J. T. ROTENBERRY. 1981. Habitat associations and community structure of birds in shrubsteppe environments. Ecol. Monogr. 51:21–41.

WIENS, J. A., J. T. ROTENBERRY, AND B. VAN HORNE. 1987. Habitat occupancy patterns of North American shrubsteppe birds: the effects of spatial scale. Oikos 48:132–147.

ZAR, J. H. 1984. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.